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Within-niche pace of life acceleration as a fundamental evolutionary principle: a mammal pilot test case

Clauss, Marcus ; Müller, Dennis W H ; Codron, Daryl

Abstract: Background: In the competition for resources, an evident mechanism by which a taxon or clade can prevail is by out-reproducing competitors, or, in other words, by a faster life history. Hence, for organisms that share a certain niche space, there should be strong directional evolution of life history characteristics towards faster reproduction. One reason why this mechanism is rarely considered may be the conceptualization of life history strategies as a set of trade-offs subjected to fixed overall physical laws, rather than as a set of morphophysiological adaptations that may evolve towards a higher efficiency. Hypothesis: Among extant taxa, directional evolution towards a faster reproduction should be reflected in a higher diversity in those clades of a niche that have a faster pace of life. Assuming phylogenetic inertia in the pace of life, fossil representatives of clades whose extant representatives are characterized by a slower pace of life should have been replaced in their niche by representatives of clades whose extant representatives have a faster pace of life. Data description: We use life history data from extant eutherian mammals from the PanTheria database, and examples from the mammalian fossil record, focusing particularly on large herbivores. Pilot results: We showcase examples that indicate differences in offspring production per unit time in eutherian mammals of similar niches; e.g., the sequence of gestation period length in which cattle, horses, dromedaries and okapis produce offspring of similar number, size and maturity (280, 340, 390 and 440 days, respectively) reflects the current species diversity and past displacement sequences of bovids, equids, camelids and giraffids. Conclusion: The demographic mechanism of the 'survival of the fittest' can be expected to have consequences on the evolution of properties determining demographic life history. Considering life history as clade-specific, and life history characteristics of extant species as a snapshot in evolutionary time, can prominently enhance interpretations of clade turnovers and species diversity.

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Within-niche pace of life acceleration as a fundamental evolutionary principle: a mammal pilot test case

Marcus Clauss¹, Dennis W.H. Müller² and Daryl Codron³

¹Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Zurich, Switzerland, ²Zoological Garden of Halle, Halle (Saale), Germany and ³Department of Zoology and Entomology, University of the Free State, Bloemfontein, South Africa

ABSTRACT

Background: A mechanism by which a taxon or clade might prevail is by reproducing faster than its competitors – or, in other words, by a faster life history. Hence, for organisms that share a niche space, there should be strong directional evolution of life-history characteristics towards faster reproduction. One reason why this mechanism is rarely considered may be the conceptualization of life-history strategies as a set of trade-offs subject to fixed overall physical laws, rather than as a set of morphophysiological adaptations that might evolve a higher efficiency.

Hypothesis: Among extant taxa, directional evolution towards faster reproduction should be reflected by higher diversity in those clades of a niche that have a faster pace of life. Assuming phylogenetic inertia in the pace of life, fossil representatives of clades whose extant representatives are characterized by a slower pace of life should have been replaced in the niche space by representatives of clades whose extant representatives have a faster pace of life.

Data description: We use life-history data from extant eutherian mammals from the PanTheria database, and examples from the mammalian fossil record, focusing in particular on large herbivores.

Pilot results: We showcase examples that indicate differences in offspring production per unit time in eutherian mammals of similar niches. For example, the sequence of gestation period length in which cattle, horses, dromedaries, and okapis produce offspring of similar number, size, and maturity (280, 340, 390, and 440 days, respectively) reflects the current species diversity and past displacement sequences of bovids, equids, camelids, and giraffids.

Conclusion: The demographic mechanism of the ‘survival of the fittest’ can be expected to have consequences for the evolution of properties determining demographic life history. Considering life history as clade-specific, and life-history characteristics of extant species as a snapshot in evolutionary time, can prominently enhance interpretations of clade turnovers and species diversity.

Keywords: competition, directional evolution, displacement, escalation, key innovation, life history, mammal.

Correspondence: M. Clauss, Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr. 260, 8057 Zurich, Switzerland. email: mclauss@vetclinics.uzh.ch

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NICHE SPACE AND NICHE OCCUPANCY

In traditional Darwinian scenarios, life is interpreted as a struggle for limited resources (Darwin, 1859). Organisms compete for these resources in many ways, which, simplistically, may be placed into one of two categories: (1) by evolving ecological niches (a process that can be considered to partition the existing resources) and expanding these niches (a process that may represent a re-partitioning of the resources) (Hutchinson, 1965); or (2) within these niches, by evolving higher fitness, which is linked to a demographic (Malthusian) concept of out-reproducing the competition (Darwin, 1859).

These two categories represent different challenges and opportunities, both in terms of the history of life and in its scientific conceptualization. Niche partitioning opens up a richness of questions about biogeography, or about form and function, including challenges to measure either, and leaves traces in the fossil record in the form of distinct locations and morphologies. It will be fundamentally influenced by variation in environmental conditions; this variation has been termed the ‘court jester’ (Barnosky, 2001) to underline its fortuitous, erratic nature. Nevertheless, a specific morphophysiological solution may not only prove to be generally suited for a certain niche space and occur convergently – presented for marsupials and eutherians (Springer *et al.*, 1997), and within the Eutheria for Afrotheria and Laurasiatheria (Springer *et al.*, 2004) – but even to be of a more general adaptiveness and hence may be, once emerged, selected for as a (non-teleological) directional ‘evolutionary trend’. How such trends can be defined, and to what degree they actually exist, has been a major bone of contention in evolutionary biology (Gould, 1988a).

The partitioning of niche space, and the expansion into empty niche space, is mainly responsible for, and quantitatively linked to, tetrapod diversity (Sahney *et al.*, 2010). The perception of directionality in niche diversification and expansion may be linked to an asymmetrical starting point, such as with the evolution of complexity from unicellular organisms, or of body or brain mass from small, small-brained ancestors; a perceived directionality towards complexity, large body mass or large brains is then only an effect of increasing variance (Gould, 1988b).

The demographic competition within a niche space, on the other hand, has received less attention. Arguably, competition for a limited resource is at the core of the Darwinian ‘survival of the fittest’, which can more aptly be worded demographically as the ‘survival of those that produce more reproducing offspring faster’ within the niche space. The replacement of slowly-reproducing occupants of a stable niche by faster-reproducing taxa should be an evident example of evolutionary directionality, termed, for example, ‘evolutionary progress’ by ‘incumbent replacement’ (Rosenzweig and McCord, 1991), or ‘escalation’ (Vermeij, 1994). Sometimes – when the faster-reproducing taxon pushes the slower-reproducing taxon to those edges of the latter taxon’s niche space that are too resource-constrained to allow the former taxon’s ‘escalated’ reproduction (Vermeij, 1994) – this process can be considered another way of niche partitioning. Importantly, life-history directionality is not constrained by the ‘perception of increasing variance’ mentioned above; theoretically, taxa can evolve in both directions, i.e. to become slower or faster. If one wanted to refute directionality in life-history evolution as we present here, one would have to find examples where, within a given (not deteriorating) niche, taxa prevail that decrease their reproductive turnover compared to their competitors.

There is no single morphological or physiological adaptation that will facilitate increased demographic fitness of a taxon. Conceptually, any adaptation that enhances the rate of reproducing offspring production could contribute to a higher fitness: from a more efficient locomotor system to a more efficient harvesting and digesting of prey; from higher growth rates to more efficient energy and nutrient transfer from mother to offspring; from increased neonate immune

competence to efficient protective parental care. Such adaptations fit the definition of ‘increased fitness’ – key innovations that do not facilitate expansion into new ecological niches but facilitate a more efficient use of the same niche (Rosenzweig and McCord, 1991; Heard and Hauser, 1995). The morphological traces that such adaptations might leave in the fossil record are most likely impossible to analyse systematically. In extant organisms, the demographic fitness of a taxon is mainly measured in an integrative fashion (without specifying the responsible physiological processes) in terms of its life-history characteristics.

LIFE HISTORY: FIXED RULES OR SNAPSHOTS IN EVOLUTIONARY TIME?

Narratives of ‘evolving adaptations’ often do not clearly separate the two concepts of niche partitioning and expansion on the one hand, and niche occupancy demographics on the other, but mostly focus on the former. Mammalian life-history studies, including the classification of species along a slow–fast continuum (Promislow and Harvey, 1990), represent a classic example.

Some time ago, Cole (1954) mentioned the potential of life-history strategies to explain competition scenarios. And differential fecundity has been at the core of some theories explaining the success of eutherians over marsupials (Lillegraven *et al.*, 1987; Hsu *et al.*, 1999). But the concept has not been expanded to other comparisons among mammals. Although life-history patterns are strongly linked to mammalian phylogeny (i.e. differ systematically among taxonomic groups), ecological correlates with the continuum have not been identified – that is, slow and fast pace of life occurs across different ecological (e.g. dietary) niches (reviewed by Gaillard *et al.*, 2016) – which suggests that mammal clades could be competing via life history within their niche space. Directionality in life-history evolution may be thought of as evolution towards a ‘Darwinian demon’ – a hypothetical, impossible organism that optimizes all fitness traits, such as producing reproducing offspring directly after being born, at infinitesimally short breeding intervals, forever (Law, 1979).

However, variation in life-history characteristics has traditionally been considered as a means by which taxa diversify into different niches (that are, for example, characterized by different mortalities) and hence partition niche space, but not as a means by which taxa compete within niche space. Life-history characteristics are represented as outcomes of fixed physical laws in the context of the metabolic theory of ecology (Brown *et al.*, 2004; Hamilton *et al.*, 2011; Sibly *et al.*, 2012). These laws make a Darwinian demon an impossibility by constraining the allocation of resources to different physiological mechanisms that serve growth, reproduction, or survival. Historically, life-history theory has emphasized the concept of trade-offs between these fitness components (Schrempf *et al.*, 2017). Taxa are categorized into different ‘pace of life’ strategies that solve the dilemma of resource allocation to the different fitness components in different ways (Promislow and Harvey, 1990; Bielby *et al.*, 2007), and thus partition niche space (Sibly and Brown, 2009; Sibly *et al.*, 2014). Life history is understood as an adaptation to ecological niches characterized in particular by the mortality they inflict on their occupants (Promislow and Harvey, 1990; Sibly and Brown, 2007; Sibly *et al.*, 2014).

Another important aspect of life-history evolution often goes unnoticed, i.e. organisms may evolve means by which life history trade-offs may be changed (Rosenzweig and McCord, 1991). Organisms might evolve, for example, so that they can have a faster growth at a lower reduction in reproductive investment – by becoming ‘more efficient’. Ignoring or denying this possibility, by explicitly or implicitly fostering the assumption that trade-offs represent physical laws, may unduly restrict our understanding of evolution, and could be compared to claims that when feeding your chicken, you have to give it more food for a longer period of time to

produce more meat, thus ignoring the possibility that someone might breed a chicken line that grows faster with the same amount of food, or even with less food (Bennett *et al.*, 2018).

In our case it may be compared to the concept that there is always a trade-off between reproduction and longevity, and that a measure integrating all individual life-history components (such as ‘lifetime reproductive effort’) is constant across taxa, with variation mainly due to measurement error (Charnov *et al.*, 2007). This conceptualization ignores the possibility that ‘high-quality’ individuals may reproduce more and live longer than their conspecifics, and may pass on this trait to their offspring.

Apart from the achievements in domestic plant and animal breeding of higher yields per investment (Floros *et al.*, 2010), empirical evidence suggests that the trade-off between reproduction and longevity, seemingly evident in interspecific comparisons, may not always apply. Thus in humans (Mitteldorf, 2010), zoo primates (Tidière *et al.*, 2017), zoo equids (Ibler and Fischer, 2017), and eusocial insects (Blacher *et al.*, 2017; Kuszewska *et al.*, 2017; Schrempf *et al.*, 2017), we see rather a positive correlation between number of reproductive events and longevity, which suggests that differences between individuals do not inhere in how they solve the dilemma of resource allocation to the trade-off fitness components, but in their overall fitness. Only when reproduction is artificially prevented in some individuals that are randomly chosen (and hence of potentially similar fitness quality as the control group) can one demonstrate the longevity-reducing effect of reproduction (Kirkpatrick and Turner, 2007; Blacher *et al.*, 2017). Given such intraspecific variation, taxa with different efficiencies in metabolic processes might evolve, and scaling relationships between biological characteristics of extant taxa might therefore represent snapshots in evolutionary time rather than outcomes of physical laws (Fritz *et al.*, 2009; Pontzer and Kamilar, 2009; Clauss *et al.*, 2014). Actually, recent studies on humans and great apes indicate acceleration of the pace of life in humans at no associated costs in longevity as one of the key components of human biology (Pontzer *et al.*, 2016; van Noordwijk *et al.*, 2018).

A SET OF PREDICTIONS

Directional evolution towards a faster pace of life should involve clear life-history effects. When following the widespread convention of comparing life-history measures on the basis of body mass, due to the overarching association between body mass and basically any quantitative characteristic of organisms (Calder, 1984; Sibly *et al.*, 2012) as well as its relevance for niche partitioning (Hutchinson, 1959), organisms should evolve towards reducing the time required to produce offspring (for their body mass), increasing their reproductive lifespan (for their body mass), increasing the number of offspring (for their body mass), and – assuming a positive link between offspring size and offspring survival, or between offspring size and the time to first reproduction – increasing the size of offspring (for their body mass) (Fig. 1A). However, with our hypothesis that life-history evolution is all about being faster, we suggest that competitors for a niche should produce more and/or larger offspring in less time (Fig. 1B), and that a unit of time is the most appropriate basis for comparison among organisms of a specific niche.

THE EUTHERIAN MAMMAL TEST CASE

We consider the set of extant species as organisms in the process of directional evolution towards a faster pace of life. Assuming that species diversity within a clade is a measure of success of that clade’s properties, and assuming that the peak diversity of a clade is shaped by biotic competition

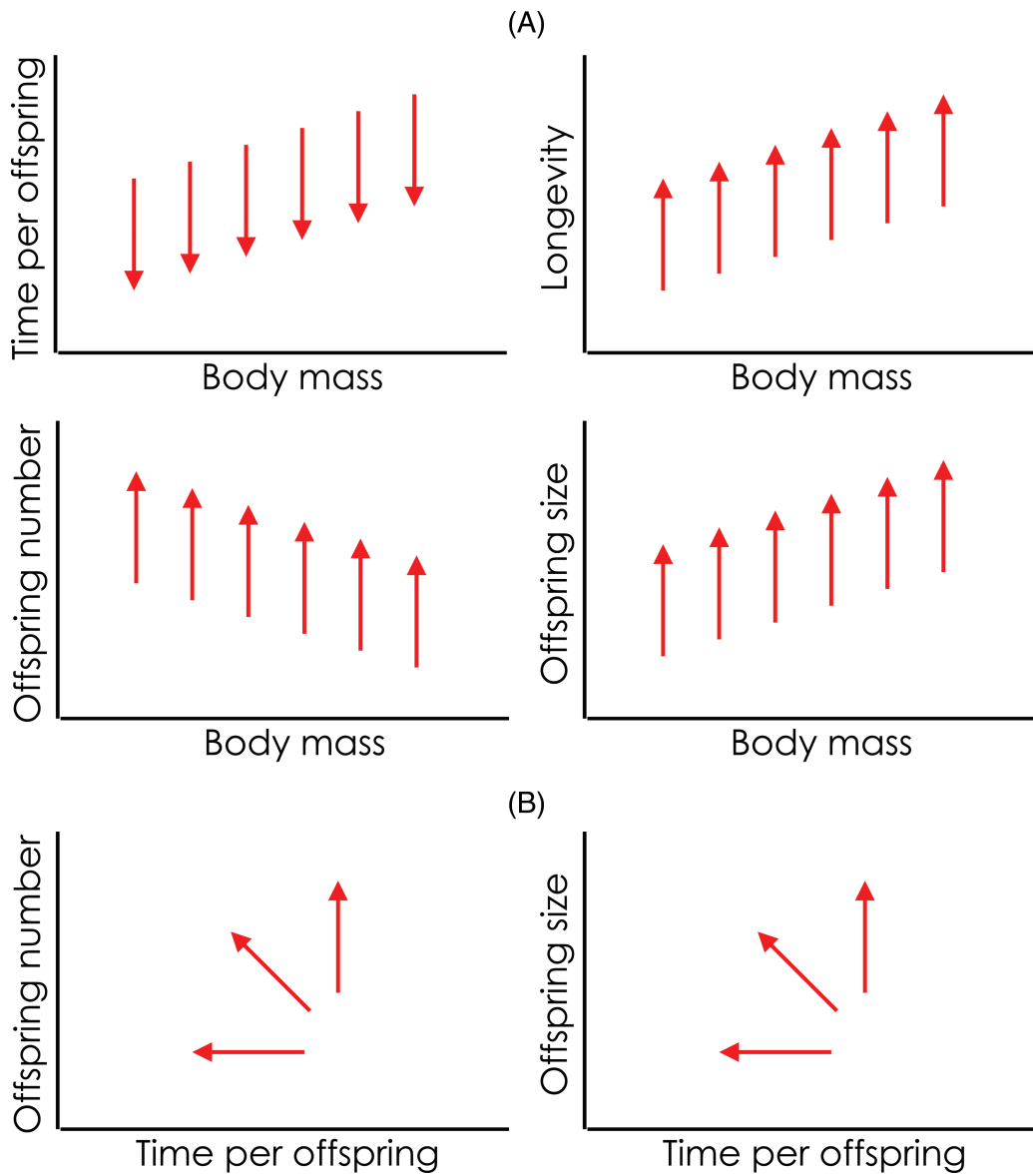


Fig. 1. Predicted directionality of directional evolution towards a faster pace of life (A) using body mass as the basis for comparison, as conventionally done in life-history data compilations, and (B) using a measure of time as the basis for comparison. Predictions relate to animals of a similar niche. Note that scenarios in (B) suggest a shortening of the time required to produce an offspring, or an increase in the number of offspring in a unit of time, or both. Over evolutionary time, relationships are predicted to change in the directions indicated, making a single dataset at any point in time (such as a set of extant animals) a snapshot that will give a different picture compared to a dataset taken at another point in time.

(Žliobaitė *et al.*, 2017), we expect large extant diversity in clades with a set of currently strong competitive properties, and a lower extant diversity in clades with currently weaker competitive properties (Gould *et al.*, 1987). The clades with weaker competitive abilities may well have a higher diversity in the fossil record. Specifically, as regards eutherian mammals, we expect the two large, less speciose superorders – Afrotheria and Xenarthra – to have a slower pace of reproduction than the speciose clades of Euarchontoglires and Laurasiatheria.

We use the PanTheria database (Jones *et al.*, 2009) as a source for mammalian life-history data. We do not consider data quality to be consistent across all measures in the dataset. While data for body mass, gestation period, neonate mass, or litter size may be of a comparatively higher quality, data for maximum longevity, interbirth interval, or litters per year may be of a lesser quality (with the latter two sometimes even in evident contradiction in the database). Hence, we expect the clearest signal for directional evolution towards a faster pace of life to be seen in the gestation period–litter mass relationship (where litter mass = neonate mass \times litter size), and a less clear signal for the longevity–hypothetical lifetime offspring number relationship [calculated as (maximum longevity – age at first reproduction)/gestation period, with or without data for the interbirth interval]. We expect the highest data quality in the largest terrestrial – and hence most easily observable – taxa. We did not systematically check and correct the database, but based on our own interest in sloths (one of us works at a zoo that keeps an international sloth studbook), added gestation period data for *Bradypus* species from the literature (Lara-Ruiz and Chiarello, 2005; Hayssen, 2009, 2010).

We graph the data for body mass–gestation period and the gestation period–litter mass relationship for some eutherian mammals, loosely grouped by niches: (1) those including arboreal folivores (sloths and primates); (2) non-fossorial insectivores (tenrecs, elephant shrews, aardvark, anteaters, armadillos, pangolins, hedgehogs, hairy hedgehogs, shrews); and (3) fossorial insectivores [‘moles’, the golden moles (*Chrysochloridae*) and the moles, shrew moles, and desmans (*Talpidae*)]. We predict that the more speciose groups will have a faster mode of reproduction than the others. For the large herbivores (elephants, hyraxes, equids, tapirs, rhinos, camels, hippos, and different ruminant families), we graph data in more detail with respect to the individual predictions of Fig. 1.

For groups including arboreal folivores (Fig. 2A) and non-fossorial insectivores (Fig. 2B), the more speciose groups (primates, shrews) have the comparatively shorter gestation periods, and achieve similar total offspring masses in shorter gestation periods than the less speciose groups. The unexpectedly long gestation periods of the afrotherian tenrecs have been commented upon previously (Symonds, 2005). A similar picture is evident in the fossorial insectivores (Fig. 2C) but the database is extremely limited. In the large herbivores, the most speciose group of the non-giraffid ruminants (cervids and bovids) has shorter gestation periods for their body size than all other taxa except the hippos (Fig. 3A), has shorter maximum longevity for their body size (Fig. 3B), produces more hypothetical offspring for their body size (Fig. 3C), and does not stand out with respect to the total neonate mass for their body size (Fig. 3D). When comparing their life-history characteristics against time, they achieve the same neonate mass in shorter gestation periods than all other taxa, again except the hippos (Fig. 3E), and achieve the same number of hypothetical lifetime offspring in a shorter lifespan (i.e. faster) than other taxa (Fig. 3F). The same picture prevails when calculating both the mass of the hypothetical or the actual lifetime offspring mass (i.e. without or with accounting for interbirth intervals, with a reduced dataset in the latter case due to the difficulty of accurately determining this particular life-history measure) (Fig. 3G,H). Seemingly, non-giraffid ruminants have evolved mechanisms to produce offspring faster than other large herbivores.

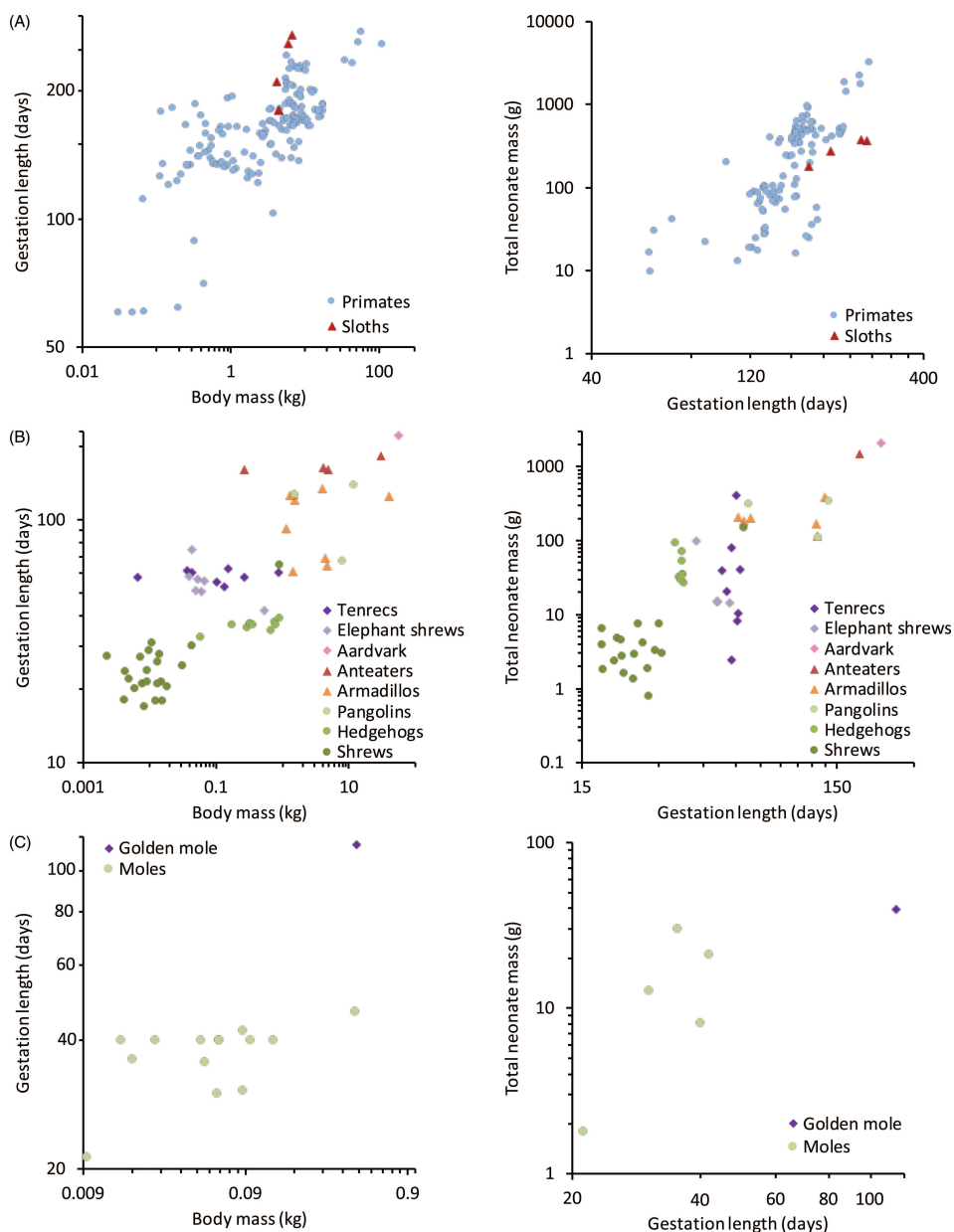
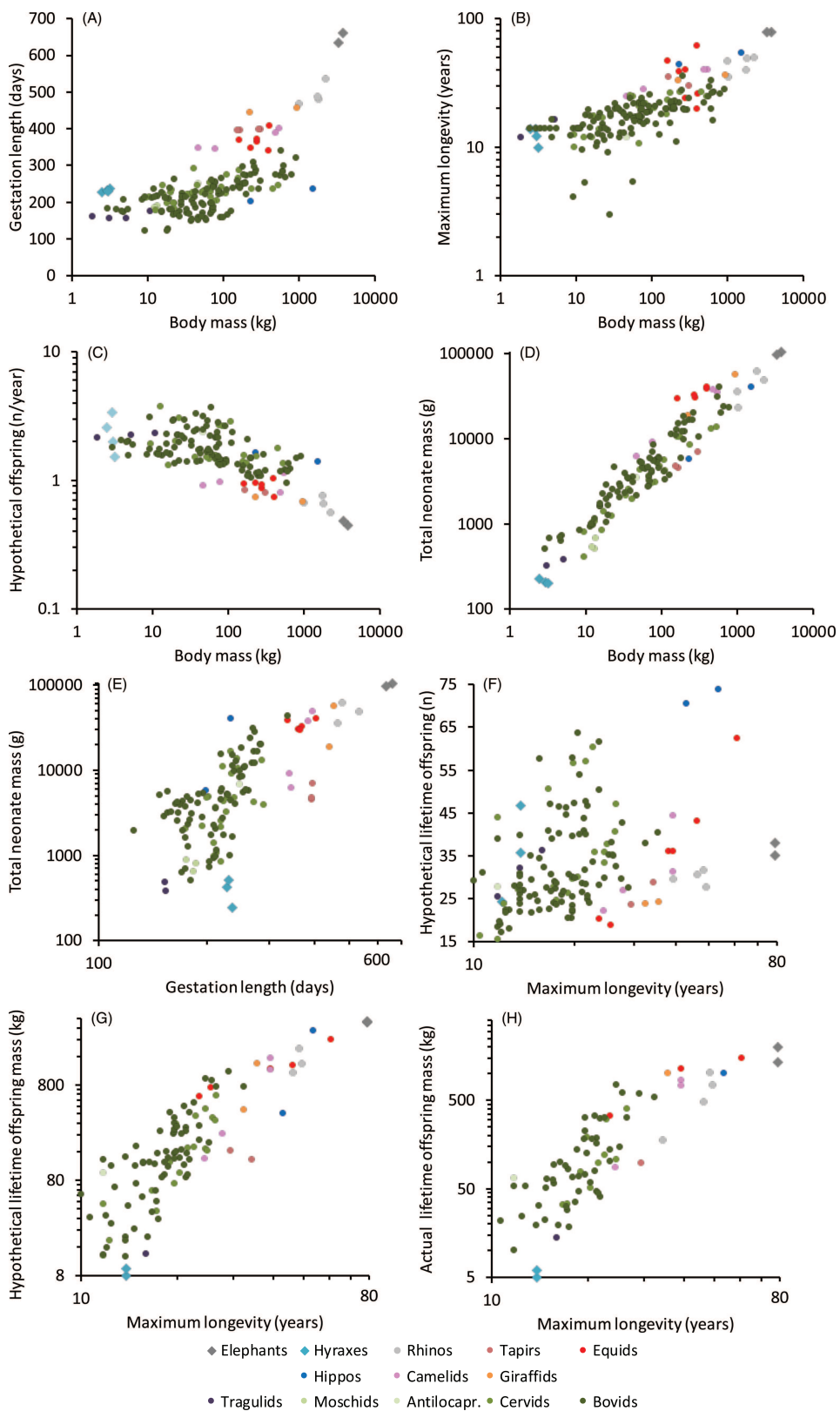


Fig. 2. Plots of (A) groups containing arboreal folivores (sloths, primates), (B) non-fossorial terrestrial insectivores (tenrecs, elephant shrews, aardvark, anteaters, armadillos, pangolins, hedgehogs, shrews), and (C) fossorial insectivores (golden moles and moles) for the gestation length–body mass relationship (left column, corresponding to a prediction in Fig. 1A) and the total neonate mass (neonate mass \times litter size)–gestation length relationship (right column, corresponding to a prediction in Fig. 1B). Afrotheria marked by diamonds in shades of purple, Xenarthra by triangles in shades of brown, Euarchontoglires by circles in shades of blue, Laurasiatheria by circles in shades of green. Note that, in general, Euarchontoglires and Laurasiatheria comprise species with comparatively short gestation periods for their body size, and that species of these groups attain similar total neonate masses at shorter gestation periods than others – a difference particularly backed by current data for the comparison of tenrecs and elephant shrews vs. hedgehogs and shrews in (B). Note that the differences are not due to a simple dichotomy of precocial and altricial young.



The graphs have several deficiencies. We have not exhaustively checked for further available data nor have we verified them independently. Moreover, we have not rigorously defined ecological niches (in the sense that we use the concept). Yet they support our hypothesis very suggestively. In particular, they suggest that at least among eutherian mammals occupying a niche, offspring size might be less linked to species diversity than to the time required to produce the offspring.

LIFE HISTORIES AS TAXON CHARACTERISTICS

That life-history characteristics are conserved within clades is central to, and appears evident from, the above assessment. A number of analyses show that life-history traits have a strong phylogenetic signal (Duncan *et al.*, 2007; Clauss *et al.*, 2014; Lemaître *et al.*, 2014; Gaillard *et al.*, 2016), leading Stearns to conclude in 1983 that ‘morphological design, in addition to size, may constrain life-history evolution’. Impressive examples from domestic species, which involve breeds ranging dramatically in body size, show hardly any variation in gestation length (Kirkwood, 1985; Heck *et al.*, 2017). However, there are differences in the phylogenetic level at which certain life-history traits are grouped (Stearns, 1983). For example, a comparison of gestation periods and longevity across mammals (Lemaître *et al.*, 2014) indicated that, within taxa, diversification in longevity exists that is not equalled by similar diversification in gestation period. And in the case of domestic animal breeds of varying size, the constancy of gestation period is evidently not equalled by a constancy in neonate mass. Yet, no systematic investigation exists on how these different life-history traits are distributed over phylogenetic levels. Neither did anyone investigate how these differences might influence the distribution of integrated life-history measures (such as generation time or population growth rate) across phylogenetic levels.

The examples we present above corroborate the general hypothesis that among eutherian mammals, Afrotheria and Xenarthra are characterized by a comparatively slow life history compared to their ecological counterparts among Euarchontoglires and Laurasiatheria. Swihart (1984), in a study concerned mainly with lagomorphs, presented a similar finding; when comparing mammalian orders for the relationship of maternal reproductive investment and foetal growth rate, he found that, at similar investment, Afrotheria and Edentata had lower foetal growth rates than all boreoeutherian orders (except primates). There are also examples

Fig. 3. Plots of large terrestrial herbivore taxa for predictions derived from Fig. 1. Note that the currently most speciose groups (cervids and bovids) have (A) comparatively short gestation periods for their body mass compared to all other groups except hippos, (C) achieve a comparatively high number of hypothetical offspring per year, (E) produce a comparable amount of neonate mass in a shorter period of time, and (F) achieve a comparable number of hypothetical lifetime offspring with a shorter maximum longevity. Even when accounting for offspring mass, for which no evident differences between taxa are evident (B), cervids and bovids produce the same (G) hypothetical lifetime offspring mass (without accounting for interbirth intervals) or (H) actual lifetime offspring mass (accounting for interbirth intervals, a measure that is available for fewer species) comparatively faster. Note that plots (E) to (H) ignore niche differentiation by body mass, being most informative for the comparison of cervids and bovids with equids, tapirs, camelids, and giraffids. Note that no calculations using maximum longevity for lifetime offspring account for reproductive senescence. Also note that some data patterns in log-log plots such as (B, C, E, G, H) are curvilinear. Rather than interpreting such patterns as indicating a physiological effect due to physical principles, we suggest that they occur because of directional evolution towards a faster pace of life that differs between clades.

of relevant differences within the Boroetheria. An impressive example is the difference in gestation period between more or less similar-sized large herbivores (Clauss *et al.*, 2014), where cattle, horses, dromedaries, and okapis produce precocial offspring of similar maturity at gestation periods of 280, 340, 390, and 440 days, respectively. Moreover, this sequence correlates with the current number of species of bovids, equids, camelids, and giraffids. The physiological mechanisms for these differences remain unidentified. They may lie in the morphology of the nutrient-delivering placenta (Baur, 1977; Capellini *et al.*, 2011; Lewitus and Soligo, 2011; Klisch *et al.*, 2017), and in a plethora of mechanisms determining nutrient and energy acquisition and use.

MEASURING LIFE-HISTORY CHARACTERISTICS

Some life-history data represent morphophysiological properties of taxa, such as gestation periods, which are comparatively fixed. Others, however, may also represent a mixed signal of intrinsic properties and specific abiotic (e.g. resource availability) and biotic (e.g. predation, density dependence) ecological interactions, in particular if these measures are derived from life tables. Ricklefs and Wikelski (2002) stated that ‘life history should be least apparent in the life table of the population [e.g. measures related to mortality], where the direct influence of the environment is greatest. It should be most apparent in traits, such as growth rate . . . , which, for highly homeostatic organisms . . . , are relatively uninfluenced by the environment, albeit not completely’.¹ There is ‘ecological compensation’ in life tables: because ‘mortality, growth and birth rates cannot vary independently in stable populations, environmental change of one variable must be accompanied by compensatory variation of another’ (Sibly and Calow, 1987). Life tables thus represent specific ecological situations because controlled, interaction-free studies are mostly infeasible for life table measurements. Even measures that sound, due to their terminology, as if they represented intrinsic physiologic properties of species – such as ‘generation time’ (Gaillard *et al.*, 2005) or ‘intrinsic rate of increase’ (Partridge and Sibly, 1991) – are calculated using empirical and hence situation-specific measures of age-dependent survival/mortality. Although we may suspect that a certain component of mortality is intrinsic, extrinsic factors play a dominant role, evidenced, for instance, by the fact that in more than 80% of all known cases, life table-derived longevity is higher for zoo populations than for populations of the same mammal species in the wild (Tidière *et al.*, 2016).

Furthermore, environmental factors are often included in productivity life-history measures. A taxon may have particularly high intra-uterine and juvenile growth rates and hence theoretically short interbirth intervals and generation times but may nevertheless have been subject to selection favouring triggers that prolong interbirth intervals to compensate for environmental seasonality. Using the factor ‘number of litters per year’ in the calculation of productivity (e.g. Charnov *et al.*, 2007; Hamilton *et al.*, 2011; Sibly *et al.*, 2014), also implicit in Fig. 3H, represents a conceptual approach which assumes that seasonal effects are an intrinsic property of the species’ pace of life. This may be justified, for example, if one assumes that times of reproductive stagnation spare resources that can be used in the following spring or over a lifetime. But then evolved adaptations to seasonal environments might prolong the time over which a certain lifetime reproductive output is reached and artificially make seasonal species appear ‘slower’ in their pace of life, even though they show acceleration in other life-history traits [for example, shorter gestation periods than expected for their size (Zerbe *et al.*, 2012; Heldstab *et al.*, 2018)]. To characterize and rank taxa, it may be appropriate to compare not only real life table-derived life-history measures, but also hypothetical measures assuming neither biotic nor abiotic interactions but

only the morphophysiological potential. In the example of the large herbivores in Fig. 3G and 3H, both approaches indicate a similar pattern.

Life-history data from zoo populations may be of particular value in this respect. For many species, a quantitative measure of seasonality (Zerbe *et al.*, 2012; Heldstab *et al.*, 2018) or neonate mortality (e.g. Debyser, 1995) will be available only for zoo populations. Similarly, existing data collections on mammalian growth rates rely heavily on data from captive animals; in Grady *et al.* (2014), for example, the ratio of mammal species with growth data from the wild versus data from captivity is 57:101 (64% zoo data). Important life-history data, such as neonate mass, age at weaning, age at first reproduction, and growth rates, can be supplied from observations in zoo animals, and efforts to supplement databases systematically with high-quality zoo data are currently under way (Silva *et al.*, 2016).

POTENTIAL APPLICATION TO INTERPRETING THE FOSSIL RECORD

The evolution of a faster life history has been at the core of recent theories on the evolution of therapsids (Botha-Brink *et al.*, 2016) and birds (Yang and Sander, 2018). Under the assumption that life-history characteristics, shown to contain a strong phylogenetic signal among extant species, are conserved within taxa and can be ascribed to fossil relatives, the question arises whether displacement sequences in the fossil record exist that do or do not match the ranking based on extant species. Consider the displacement of the diverse Early Tertiary African hyracoid fauna, which had body sizes from <5 kg (extant hyraxes) up to rhino-sized species, by other ungulate taxa (Schwartz *et al.*, 1995). Indeed, the gestation periods of extant hyraxes [7 months or 230 days (Millar, 1971)] are astonishingly longer than those of similar-sized lagomorphs [less than 2 months (Swihart, 1984)] or similar-sized ruminants [dik-dik, *Madoqua* spp., 166–174 days (Kingswood and Kumamoto, 1997)]. In the opposite direction, the body sizes of fossil proboscideans ranged from fox-size to mammoths (Shoshani and Tassy, 2005; Gheerbrant and Tassy, 2009). But they declined to a few relict species in the wake of the diversification of other large herbivores, and what remain have comparatively long gestation periods (elephants, 22 months, compared to 16–18 months in rhinos and 9–11 months in large bovids). Long gestation periods are apparently a common feature of afrotherians. Another evident afrotherian candidate for such displacements would be the Macroscelididae by omnivorous rodents (Hooker and Collinson, 2012). And one might speculate that were it not for the clear geographical separation of golden moles and talpids (Nevo, 1979), the long gestation period reported for the former could make it susceptible to displacement by the latter group, which has shorter gestation periods. The apparent historical displacement of camelids and equids by ruminants (Janis, 1989; Janis *et al.*, 1994), and the apparent displacement of giraffids by bovids and cervids (Clauss and Rössner, 2014), both match the differences in gestation length between extant bovids, camelids, equids, and the surprisingly long gestation periods in giraffids (Fig. 3A). In addition, bovids and cervids achieve a similar number and mass of lifetime offspring in shorter time (Fig. 3F, G, H).

CONCLUSION

We consider comparative data compilations not only as indicators of morphophysiological adaptations to a variety of niches, but also as snapshots of historical and ongoing evolution. This perspective may enhance our understanding of the scatter in such compilations. In particular, one may use a life-history proxy as an indicator of the pace of life, then incorporate that proxy as a

covariate. We believe that strategy may increase the explanatory power of comparative datasets (Pontzer and Kamilar, 2009), in particular when ecological niches are also considered.

The use of the concept of directionality in evolutionary biology has been heavily criticized as being ‘only a *post hoc* adaptive story’ that is ‘in no way predictive of future trends’, and ‘a tautology’ that identifies ‘the later animal (the “winner”) as a “superior competitor”’ (Benton, 1987). This view may be an understandable reaction to narratives that explain directionality in terms of a single or a few anatomical features. But if we consider that animals within a given niche space compete via life-history-dependent demographics, then we have not a *post hoc* explanation, but a prediction logically derived from the demographic component of the theory of Darwinian evolution. Directional evolution towards a faster pace of life is the answer to Benton’s (1987) statement that ‘it is hard to envisage a constant competitive advantage that lasted so long and persistently favoured all of the species of one large taxon against all of the species of another in all environments’.

The examples from eutherian mammals indicate that directional evolution towards a faster pace of life may well be an important component of mammalian evolutionary history. In line with Gould’s (1990) caveat that one should not semantically confuse evolutionary directionality with a (wrongly assumed) continuous process of directional change within a clade, we state that rather than becoming faster at reproduction, slower-reproducing clades tend to be replaced by faster-reproducing clades [thus, incumbent replacement *sensu* Rosenzweig and McCord (1991)]. The mechanism of incumbent replacement might also be fruitful for other groups at all taxonomic levels, including plants. We note that the morphophysiological causes for differences in the pace of reproduction are not well explored. For example, consider that cattle can produce offspring of similar number, size, and maturity as do horses in about 20% less time. But the underlying mechanisms that lead to that difference have never been investigated. Yet, such mechanisms might be as important in evolution as basal metabolic rates or dental morphology.

Characterizing species by life-history measurements is a task that should not be considered finished, given the nature of currently available datasets (Silva *et al.*, 2016). Using observations from animals under human care could serve as a surrogate for ‘control’ studies. These would aim to measure intrinsic life-history properties of species, as opposed to properties derived from life tables in natural environments that necessarily represent integrated measures of the species’ intrinsic capacities and the biotic and abiotic influences on the particular population under study.

We cannot scale the evolutionary significance of life-history differences compared to other mechanisms,² and we also do not make claims as to what degree environmental triggers, with their subsequent changes of niche space, are necessary [as ‘turnover pulses’ *sensu* Vrba (1993)] to let life-history differences between clades take full effect. Yet, acknowledging that clades adapted to similar niches can differ dramatically in their pace of life can fruitfully add to interpretations of faunal turnover and diversification, potentially often resolving the seeming dilemma that taxa are now absent from geographical or climatic environments in which their fossil relatives once persisted – in other words, from habitats that cannot be claimed to be generally unsuitable for their clade.

On the other hand, the perseverance of clades of a comparatively slow pace of life, such as the afrotherians in their respective niches, also requires explanation. Important counter-arguments against the generality of directional evolution towards a faster pace of life would be documentation of the (local) displacement of clades considered fast-reproducing today, such as cervids or bovids, by clades using the same niche that are considered slower-reproducing today, such as tapirs or small rhinos.

Finally, the use of words that indicate directionality, like ‘directionality’ itself, ‘trend’, ‘escalation’, ‘arms race’, or ‘increasing efficiency’, should not be confused with a concept of ‘progress’ that has teleological meaning (Gould *et al.*, 1987; Gould, 1988a). True, evolutionary biology rightfully wants to distance itself from the naturalistic fallacy of equating any observation of directionality with elation over progress or a *scala naturae*. Nonetheless, it should not refuse, or refuse to test, the concept of directionality as such.

NOTES

1. Actually, even growth rates can differ dramatically within mammal species depending on the available resources (Leigh, 1994; Glogowski *et al.*, 2018; Schiffmann *et al.*, 2019).
2. Considering the present state of the planet with the single species *Homo sapiens* outnumbering all wild mammals by far in terms of biomass (Bar-On *et al.*, 2018), one can argue that rather than accelerating the pace of life or evolving any other measure that represents a reactive adaptation to the properties of a niche, evolving the capacity to actually control resources at landscape (and finally planetary, i.e. multi-niche) scale represents another level of non-teleological directionality in organismal evolution. Inherently, this capacity reduces niche space and niche partitioning across species, but leads to increased diversification and niche partitioning within the controlling species. So to speak, man has become a real ‘Darwinian demon’ (Rosenzweig, 2005), not by evolving a high efficiency of resource use (as in traditional ‘adaptations’), but by evolving extreme efficiency in resource control.

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